

**Shark Bowl Working Document  
SB/02/11**

**A SIMPLIFIED BAYESIAN DELAY-DIFFERENCE MODEL:  
APPLICATION TO LARGE COASTALS**

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June 2002

**Summary**

A simplified delay-difference model (lagged recruitment, survival, and growth; LRSG) state-space model was used to model the dynamics of the large coastal shark complex and sandbar and blacktip shark stocks. This model takes into account the lag between birth and subsequent recruitment to the adult stock, as well as growth and natural mortality, and the stock recruitment relationship. Bayesian statistical techniques were used to fit the model using a Markov Chain Monte Carlo (MCMC) method for numerical integration. In this approach, a state-space model accounts for both process error and observation error in a unified analytical framework that uses Gibbs sampling to sample from the joint posterior distribution. Results from an implementation with the catch and catch rate series used for the 1998 shark assessment agree with those from a recent sensitivity analysis that used several stock assessment methodologies, and indicate that the 1998 biomass of the large coastal shark complex and sandbar shark was below that producing MSY, whereas the 1998 biomass for blacktip shark was above that producing MSY.

**Stock Assessment Model and Application**

A lagged recruitment, survival and growth (LRSG) model (Hillborn and Mangel 1997) was used to model the dynamics of the large coastal shark complex, sandbar, and blacktip shark. This model is an approximation of the delay-difference model of Deriso (1980) and can be expressed in its discrete form as:

$$B_{t+1} = sB_t + R_t - C_t$$

where  $s$  is a compound parameter that describes how much the biomass changes from one year to the next as a result of survivorship resulting from natural mortality causes only, and growth in mass;  $R_t$  is recruitment to the population and is expressed as:

$$R_t = \frac{B_{t-L}}{a + bB_{t-L}}$$

where the term  $t-L$  indicates that recruitment in year  $t$  depends on the biomass  $L$  years before (Hilborn and Mangel 1997), and  $L$  refers to the time lag in years between reproduction and recruitment to the fishery. It is assumed that fish become vulnerable to the fishing gear and reach sexual maturity at the same age.

The parameters  $a$  and  $b$  are defined as:

$$a = \frac{B_0}{R_0} \left(1 - \frac{z - 0.2}{0.8z}\right),$$

$$b = \frac{z - 0.2}{0.8R_0}$$

where  $R_0 = B_0(1-s)$ , and  $z$  is a parameter that represents the steepness of a Beverton-Holt stock recruitment curve, or the ratio between recruitment at  $0.2B_0$  and  $R_0$ . A high value of  $z$  ( $=0.99$ ) means that recruitment is almost constant and independent of spawning stock, whereas a low value of  $z$  ( $0.20$ ) indicates that recruitment is proportional to spawning stock.

Performance indicators used included the biomass at MSY ( $B_{MSY}$ ) and the maximum sustainable yield (MSY), which in this case are defined as:

$$B_{MSY} = \frac{1}{b} \sqrt{\frac{a}{1-s}} - a$$

and

$$MSY = B_{MSY} \left(s - 1 + \frac{1}{a + bB_{MSY}}\right)$$

Other performance indicators included the ratio of stock biomass in the current year to  $B_{MSY}$  ( $B_t/B_{MSY}$ ), the exploitation rate in the current year (exploitation rate= $C_t/B_t$ ), the harvest rate to produce MSY ( $H_{MSY}=MSY/B_{MSY}$ ), and the ratio of harvest rate in the current year to  $H_{MSY}$  (Hratio=exploitation rate/ $H_{MSY}$ ). Note that because the 1998 shark assessment used numbers instead of biomass, all abundances given here are in numbers.

State-space models can be used to relate observed catch rates ( $I_t$ ) to unobserved states (biomass,  $B_t$ ) through a stochastic observation model for  $I_t$  given  $B_t$ . A description of state-space models can be found in Meyer and Millar (1999a) and Millar and Meyer (1999). Meyer and Millar (1999b) implemented a nonlinear, nonnormal state-space model assuming lognormal error structures and a reparametrization by expressing the annual biomass as a proportion of carrying capacity ( $P_t = B_t/K$ ). In the present implementation, no reparametrization was used, i.e., the annual biomass ( $B_t$ ) was used directly. The joint prior distribution of all unobservable quantities, i.e.,  $B_0$ ,  $z$ ,  $s$ ,  $q$ ,  $\sigma^2$  (process error variance), and  $\tau^2$  (observation error variance) and the unknown states  $B_1, \dots, B_N$ , and the joint distribution of the observable quantities, i.e., the CPUE indices  $I_1, \dots, I_N$  were modeled. Bayesian inference then uses the posterior distribution of the unobserved quantities given the data (see Meyer and Millar 1999a for a full description of the model).

As in the original model developed by Millar and Meyer (1999a), the present implementation used inverse gamma distributions as priors for  $\sigma^2$  and  $\tau^2$ , but the MLEs for  $q$  in each CPUE time series were used instead of one prior for  $q$  for each series. The geometric average of the time series of individual  $q$  estimates for each CPUE series was used as an analytic solution for the estimate of  $q$  that maximizes the likelihood function (Punt 1988; Hilborn and Mangel 1997):

$$\hat{q} = e^{\frac{1}{y} \sum_i \ln \left( \frac{I_i}{\hat{B}_i} \right)}$$

where  $y$  is the number of years in each CPUE series.

The priors for the virgin biomass ( $B_0$ ) were uniform on the log of  $B_0$  as used in the 1998 shark stock assessment (0-20,000,000 individuals; note that numbers were used in the assessment instead of biomass). Priors for the catch in 1974-1980 or 1974-1985 ( $C_0$ ) were also the same as those used in the 1998 assessment. Uninformative priors were also chosen for the steepness parameter,  $z$ , i.e., a uniform distribution ranging from 0.2 (theoretical minimum) to 0.9. The prior chosen for  $s$  (the parameter combining survivorship and growth) was also uninformative. A uniform distribution ranging from 0.60 to 0.95 (large coastal complex), 0.70-1.0 (sandbar), and 0.75-1.0 (blacktip) was assumed for  $s$ , based in part on rates of annual survivorship used to calculate intrinsic rates of increase and on growth information for large coastal sharks. The time lag between birth and recruitment to the fishery ( $L$ ) was set at 13 and 7 years for sandbar and blacktip, respectively, based on estimated ages at maturity for these species. For the

large coastal shark complex,  $L$  was set at 10 years in an attempt to approximate the combined ages at maturity of the species making up this grouping.

The prior for  $\sigma^2$  was an inverse gamma distribution with the 10% and 90% quantiles set at 0.04 and 0.08, and the priors for  $\tau^2$  (one for each individual CPUE series; Form 1) were also described by an inverse gamma distribution with the 10% and 90% quantiles set at 0.05 and 0.15. In an alternative scenario (Form 2), one single value of  $\tau^2$  was used for all series and given an inverse gamma distribution. No  $CV^2$  s were used in any of the scenarios run in WINBUGS. All runs were based on two chains of initial values (where the  $B_t$  values were set equal to low and high values, respectively) to account for over-dispersed initial values (Spiegelhalter et al. 2000), and included a 5,000 sample burn-in phase followed by a 100,000 iteration phase.

## Results

Mean values and CVs of the posterior distributions for several population parameters and management benchmarks are presented in Table 1. For the large coastal complex, virgin biomass ( $B_0$ ) and abundance in 1998 ( $B_{1998}$ ) were estimated to be lower than found in a sensitivity analysis of the 1998 shark assessment (Cortés 2002) using several surplus production models. However, MSC for Form 2 (one  $\tau^2$  for all series) of the model and the ratio of abundance in 1998 to virgin biomass or carrying capacity ( $B_{1998}/K$ ) were very similar. The LRSG model estimated high values of the parameter incorporating survival and growth,  $s$ , and fairly low values of the steepness parameter,  $z$ .

For sandbar shark,  $B_0$  and  $B_{1998}$  also were estimated to be lower than found in the sensitivity analysis of the 1998 shark assessment, especially with Form 2 of the model, but MSC and  $B_{1998}/K$  were again similar. The LRSG model estimated values of  $s$  a little lower and values of  $z$  a little higher than for the large coastal complex. For blacktip shark,  $B_0$  and  $B_{1998}$  were still somewhat lower than found in the sensitivity analysis of the 1998 shark assessment, but MSC was higher for Form 2 of the model.  $B_{1998}/K$  was again very similar. The model estimated values of  $s$  and  $z$  very close to those for sandbar.

The posterior distributions of several population parameters and management quantities obtained through Form 2 of the Bayesian state-space LRSG model are shown in Figures 1, 3, and 5 for the large coastal complex, sandbar, and blacktip shark, respectively. For the large coastal complex, the posteriors for  $B_0$ ,  $B_{1998}$ ,  $B_{1998}/K$ ,  $B_{MSY}$ , and  $C_0$  were normal with a long right tail (Fig. 1). The posterior for  $s$  favored high values, but the model estimated lower values for  $z$ . For sandbar shark, most posteriors had very long right tails, but the posterior for  $z$  favored higher values than that for the large coastal complex (Fig. 3). The posteriors for blacktip shark (Fig. 5) were generally less normal than those for the large coastal complex and sandbar shark. The model also estimated higher values of  $z$  than for the large coastal complex, and values of  $s$  very similar to those for sandbar, although the shape of the posteriors differed.

Relative biomass trajectories and relative harvest rate trajectories estimated through Form 2 of the Bayesian state-space LRSG model are shown in Figures 2, 4, and

6, respectively, for the large coastal complex, sandbar, and blacktip shark. For the large coastal complex, the model predicted that relative biomass was above 1 until 1990, but that the harvest rate exceeded that producing MSY by about 3 times at the beginning of the time series to about 15-20 times towards the end of the time trajectory (Fig. 2). For sandbar shark, relative biomass was also above 1 until 1990, decreased below that level until 1996, and was above 1 again in 1997 and 1998 (Fig. 4). The relative harvest rate was estimated to range from about 1.8 in 1974 to about 4 in 1998, with higher values in the 1990's. For blacktip shark, relative biomass was well above 1 during the whole trajectory (Fig. 6). The relative harvest rate was estimated to range from about 1.2 in 1974 to a maximum of 2 in 1992, after which it decreased to 1.3 in 1998.

## References

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**Table 1.** Estimated expected values (EV) of the means and coefficients of variation (CV) of marginal posterior distributions for output parameters from the Bayesian LRSG model analysis. Results for the large coastal shark complex, sandbar, and blacktip shark are shown for two different versions of the observation error structure.

<b>Large coastal complex</b>				
<b>Parameter</b>	<b>Form 1<sup>1</sup></b>		<b>Form 2<sup>2</sup></b>	
	<b>EV</b>	<b>CV</b>	<b>EV</b>	<b>CV</b>
B <sub>0</sub>	6890	0.23	5782	0.25
C <sub>0</sub>	321	0.39	342	0.38
z	0.44	0.44	0.53	0.37
s	0.91	0.05	0.88	0.06
B <sub>1998</sub>	1486	0.34	1205	0.33
B <sub>1998</sub> /K	0.22	0.27	0.21	0.25
MSC	139	0.66	200	0.47
B <sub>MSC</sub>	2524	0.37	1846	0.38

<b>Sandbar</b>				
<b>Parameter</b>	<b>Form 1<sup>1</sup></b>		<b>Form 2<sup>2</sup></b>	
	<b>EV</b>	<b>CV</b>	<b>EV</b>	<b>CV</b>
B <sub>0</sub>	2265	1.06	1467	0.88
C <sub>0</sub>	112	0.53	105	0.50
z	0.59	0.35	0.62	0.30
s	0.86	0.08	0.83	0.08
B <sub>1998</sub>	858	1.44	461	1.18
B <sub>1998</sub> /K	0.35	0.51	0.31	0.33
MSC	87	0.93	79	0.46
B <sub>MSC</sub>	682	1.20	416	1.06

<b>Blacktip</b>				
<b>Parameter</b>	<b>Form 1<sup>1</sup></b>		<b>Form 2<sup>2</sup></b>	
	<b>EV</b>	<b>CV</b>	<b>EV</b>	<b>CV</b>
B <sub>0</sub>	9295	0.40	10250	0.47
C <sub>0</sub>	293	0.43	336	0.44
z	0.61	0.32	0.61	0.32
s	0.87	0.08	0.84	0.08
B <sub>1998</sub>	6795	0.50	8037	0.59
B <sub>1998</sub> /K	0.73	0.33	0.73	0.28
MSC	489	0.85	635	0.78
B <sub>MSC</sub>	2695	0.54	3051	0.61

<sup>1</sup> Using one MLE for q for each series, 1  $\sigma^2$ , 1  $\tau^2$  for each series;

<sup>2</sup> Using one MLE for q for each series, 1  $\sigma^2$ , 1  $\tau^2$  for all series;